

Mitochondrial DNA and Microsatellite DNA Variation in Domestic Reindeer (*Rangifer tarandus tarandus*) and Relationships with Wild Caribou (*Rangifer tarandus granti*, *Rangifer tarandus groenlandicus*, and *Rangifer tarandus caribou*)

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Reindeer (*Rangifer tarandus tarandus*) in Alaska are semidomestic livestock descended from 1280 animals introduced from Siberia, Russia, approximately 100 years ago. Genetic variation at 18 microsatellite DNA loci and the cytochrome *b* gene of mitochondrial DNA (mtDNA) was quantified in reindeer from Alaska, Siberia (Russia), and Scandinavia and compared with wild North American caribou. Mean sequence divergence among 15 mtDNA haplotypes in reindeer was 0.007 substitutions per nucleotide site, and reindeer mtDNA is polyphyletic with caribou mtDNA. Microsatellite allele and mtDNA haplotype frequencies are similar between Alaskan and Russian reindeer and differentiated between these and Scandinavian reindeer. The frequencies of microsatellite alleles and mtDNA haplotypes are different in reindeer and wild caribou (*Rangifer tarandus granti*, *Rangifer tarandus groenlandicus*, and *Rangifer tarandus caribou*). Alaskan reindeer have maintained a genetic variation comparable to that in Russia and differentiated from that of wild caribou, >100 years after their introduction to Alaska.

Reindeer (*Rangifer tarandus tarandus*) in Alaska occur in semidomestic herds descended from animals introduced from Siberia, Russia, between 1892 and 1902. After the introduction of 1280 animals, Alaskan reindeer herds increased to 5148 in 1902, 259 000 in 1922, and 600 000 in the 1930s (Stern and others

1980). The reindeer herds then decreased due to reduced management, predation, and emigration to wild caribou (*Rangifer tarandus granti*) herds to approximately 25 000 in 1950–1977 and 20 000 at present. Preliminary analyses showed limited genetic differentiation among the Alaskan and Siberian reindeer herds (Cronin, Patton, and others 2003).

Reindeer in Alaska have interbred with wild caribou on open ranges (Bailey and Hendee 1926; Rausch 1951; Stern and others 1980) and in captivity (Klein 1980). However, domestic reindeer and wild caribou in Alaska have different allele frequencies for serum transferrin (Røed and Whitten 1986), mitochondrial DNA (mtDNA), kappa casein, major histocompatibility complex genes (Cronin and others 1995), and microsatellite loci (Cronin, Patton, and others 2003), suggesting little genetic introgression in either direction. This is probably because of low fitness of hybrid animals in the wild and relatively little crossbreeding in captivity. Caribou are generally larger, have longer legs, are more wary and difficult to handle, may breed 2–4 weeks earlier, are more migratory, and may have different frequencies of antlered females than reindeer (Klein 1980; Reimers 1993; Cronin, Haskell, and Ballard 2003).

Alaskan reindeer provide interesting insights of genetic variation and differentiation at 2 levels: among introduced herds (i.e., Alaska) and herds from the geographic region



Figure 1. Distribution of reindeer herds in Alaska sampled for genetic analysis.

of origin (i.e., Siberia, Russia) and between domestic (i.e., reindeer) and wild (i.e., caribou) relatives of the same species. In this paper we quantified the genetic variation of reindeer from Alaska, Siberia (Russia), and Scandinavia and compared it with that in wild caribou. We expanded previous analyses of 7 microsatellite loci (Cronin, Patton, and others 2003) to include additional reindeer herds, microsatellite loci, and sequences of the mtDNA cytochrome *b* gene. The mtDNA is maternally inherited, and microsatellites are biparentally inherited and provide different insights into genetic variation and differentiation.

Materials and Methods

Tissue and blood samples were collected from 13 reindeer herds from 3 regions: Alaska, Russia, and Scandinavia (Figure 1, Table A1). The Alaskan herds derived from reindeer that were transplanted from Siberia, Russia, to the Seward Peninsula, Alaska. Reindeer from the Russian herds were from the Magadan district in Siberia. It is not known if these are descendants of the source stock of the Alaskan transplants, but they are from the same general part of Siberia. The Scandinavian reindeer are from Norway and

Sweden (*Rangifer tarandus tarandus*) and Svalbard Island (*Rangifer tarandus platyrhynchos*) that have been previously analyzed for genetic variation (Olsaker and Røed 1990; Røed and Midthjell 1998; Flagstad and Røed 2003). The Svalbard Island reindeer have different morphology and patterns of genetic variation than the reindeer from Norway and Sweden (Storset and others 1978; Røed and Whitten 1986; Gravlund and others 1998; Côté and others 2002).

Genomic DNA was extracted, and the mtDNA cytochrome *b* gene was amplified and sequenced for 76 reindeer representing the 13 reindeer herds (Table A1) with polymerase chain reaction (PCR) as described by Cronin and others (1999). Sequences were aligned with the program SEQUENCHER (Gene Codes Inc., Ann Arbor, MI). Nucleotide sequence divergences were calculated for all nucleotide sites and for synonymous (*ds*) and nonsynonymous (*dn*) substitutions (Jukes and Cantor 1969) with the MEGA computer program (Kumar and others 1993). We used a *Z*-test to test the hypothesis that substitutions reflect purifying selection (i.e., *ds* > *dn*). Phylogenetic relationships of the mtDNA sequences were assessed with maximum parsimony with the PAUP program (Swofford 2002). We included the cytochrome *b* sequence of representative haplotypes from 3 subspecies of wild caribou (Alaskan barren-ground caribou *R. t. granti*, Canadian barren-ground caribou *Rangifer tarandus groenlandicus*, and woodland caribou *Rangifer tarandus caribou*, Cronin and others 2005) and white-tailed deer (*Odocoileus virginianus*) as an out-group.

Genotypes at 18 microsatellite loci were determined for 145 reindeer with PCR primers developed in cattle and methods applied to caribou (Cronin and others 2005). The loci include 7 (IGF1, CRH, RBP3, BM848, BM6438, BMC1009, and CSN10) that were used previously on reindeer (Cronin, Patton, and others 2003) and 11 others (BMS574, TGLA44, BMS1788, BMS1315, BMS1247, ILSTS028, ILSTS023, BMS745, BMS468, BMS2270, and CSSM036) (Fries and others 1993; Bishop and others 1994). Some microsatellite loci are conserved between bovids and cervids (Engel and others 1996; Kuhn and others 1996; Talbot and others 1996; Wilson and others 1997; Slate and others 1998), but it is not known if these loci occur on homologous chromosomes in both families. Also, some of these loci are linked to functional genes in the cattle genome (retinol-binding protein 3 interstitial [RBP3], corticotropin-releasing hormone [CRH], kappa casein [CSN10], insulin-like growth factor IGF1) and may also be linked in the *Rangifer* genome.

The herds were pooled into Alaskan, Russian, and Scandinavian regions for data analysis. Microsatellite DNA variation was quantified including the average number of alleles per locus (*A*) and observed (H_o) and expected heterozygosity (H_e) with the MICROSATELLITE TOOLKIT computer program (Park 2001), and allelic richness (El Mousadik and Petit 1996) with the F-STAT program (Goudet 1995). Allelic richness was compared between each pair of regions with a *t*-test of the mean values for the 18 loci. The F-STAT program was used to test among loci for linkage disequilibrium and differentiation of allele frequencies among regions

with F_{st} (Weir and Cockerham 1984). The GENEPOP program (Raymond and Rousset 1995) was used to test among genotypes at each locus for Hardy-Weinberg equilibrium.

We also compared levels of variation and allele frequencies at the 18 microsatellite loci and mtDNA between the reindeer and the wild caribou analyzed by Cronin and others (2005). We calculated genetic distances (chord distance; Cavalli-Sforza and Edwards 1967) for the microsatellite loci between each group and constructed a dendrogram using the unweighted pair group method based on arithmetic averages (UPGMA; Sneath and Sokal 1973) with the BIOSYS program (Swofford and Selander 1981).

Results

Mitochondrial DNA

We obtained 1194 nucleotides of mtDNA cytochrome *b* sequence for 76 reindeer (GenBank accession numbers AY726730 and DQ673122–DQ673135) that comprised 15 mtDNA haplotypes (designated R1–R15) differing by ≥ 1 nucleotide substitutions. There were substitutions at 36 different nucleotide positions including 31 transitions and 5 transversions, and 7 of these substitutions resulted in amino acid substitutions (i.e., nonsynonymous substitutions). The mean nucleotide sequence divergence distances (Jukes and Cantor 1969) between the 15 reindeer haplotypes was 0.0069 (standard error [SE] = 0.0012) substitutions per nucleotide site. The rate of synonymous substitutions between haplotypes ($d_s = 0.0223$) was significantly greater than the rate of nonsynonymous substitutions ($d_n = 0.0013$) between haplotypes ($Z = 4.487$, $P < 0.00001$), suggesting that purifying selection occurs at this mtDNA locus. The average sequence divergence between the 15 reindeer haplotypes and the white-tailed deer haplotype was 0.1267 (SE = 0.0005).

A strict consensus tree of the mtDNA cytochrome *b* sequences (Figure 2A) of 6 equally parsimonious trees was generated (28 parsimonious informative sites, 192 steps; consistency index = 0.889, retention index = 0.924). Bootstrap values higher than 0.5 are shown above the nodes of the tree, and Bremer indices are shown below the nodes. The consensus tree includes a large clade containing all 15 of the reindeer haplotypes along with the wild barren-ground caribou haplotypes (C8, C12). The woodland caribou haplotype (C6) occurs in a separate clade. There is no geographic or subspecific structure apparent in the large clade, and the mtDNA phylogeny of reindeer and barren-ground caribou appears polyphyletic. Phylogenetic trees with similar topologies were obtained with UPGMA and Neighbor-Joining (Saitou and Nei 1987) analyses of Jukes and Cantor (1969) nucleotide sequence distances (data not shown).

The mtDNA haplotype distributions (without regard to phylogeny) indicate considerable variation among the 3 regions ($F_{st} = 0.191$, Table 1). There are 8 haplotypes in the Alaskan reindeer and 8 haplotypes in the Russian reindeer. Four of these are shared by Alaskan and Russian reindeer, with 2 predominating in both regions (R1 and R2). The mtDNA haplotype frequencies are not different in reindeer

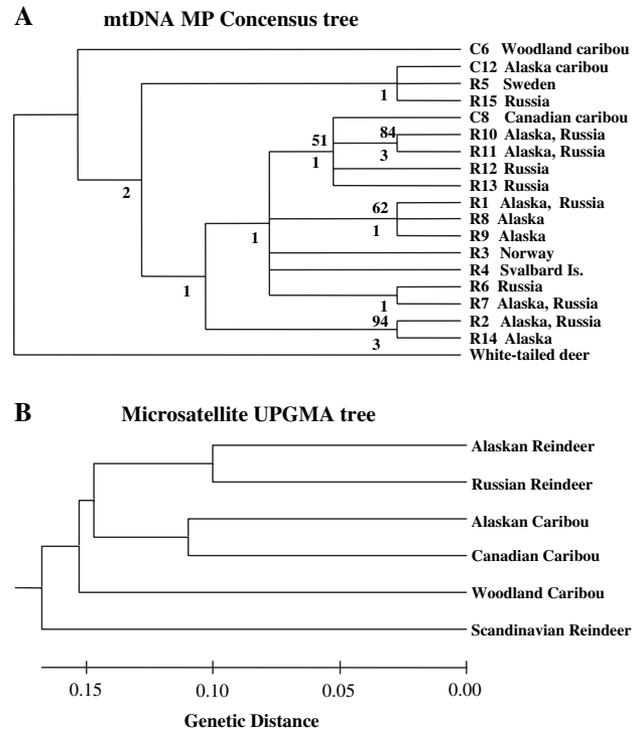


Figure 2. (A) Maximum parsimony strict consensus tree of mtDNA cytochrome *b* haplotypes in reindeer. Three haplotypes for caribou and one haplotype for white-tailed deer are included. The numbers preceded by an “R” (reindeer) or a “C” (caribou) represent mtDNA haplotypes, and locations in which haplotypes occurred are indicated. Bootstrap values >0.5 are shown above nodes, and Bremer values are shown below nodes. (B) UPGMA dendrogram of reindeer and caribou, constructed with genetic distances (Cavalli-Sforza and Edwards 1967) for 18 microsatellite DNA loci.

from Alaska and Russia ($F_{st} = -0.004$). Three haplotypes occur only in Scandinavian reindeer, resulting in significant differentiation between Scandinavia and Alaska ($F_{st} = 0.332$) and Russia ($F_{st} = 0.249$).

Microsatellites

We determined genotypes and allele frequencies for 145 reindeer at 18 microsatellite loci. Most loci are highly polymorphic, although 2 were monomorphic (ILSTS023 and CSN10) and 2 (BMC1009 and BMS1315) had only 2 alleles. Allelic richness varied from 3.66 to 3.82 and was not significantly different among the regions (Table 1). The average observed heterozygosity ranged from 0.34 to 0.39, and average expected heterozygosity ranged from 0.42 to 0.45 among the reindeer in the 3 regions. Tests among the 16 polymorphic loci showed that some loci deviated ($P < 0.05$) from Hardy-Weinberg equilibrium, including the CRH, BM848, TGLA44, and BM1788 loci in Alaska, the BM6438, BM848, CSSM036, and TGLA44 loci in Russia, and the

Table 1. Measures of microsatellite variation and numbers of mtDNA haplotypes in reindeer and caribou

	Alaskan reindeer ^a	Russian reindeer ^a	Scandinavian reindeer ^a	Alaskan caribou ^b	Canadian caribou ^b	Woodland caribou ^b
Measures of microsatellite variation						
<i>N</i>	75	51	19	78	49	29
<i>H_e</i>	0.441	0.424	0.454	0.502	0.491	0.490
<i>H_o</i>	0.387	0.380	0.339	0.461	0.437	0.367
<i>A</i>	5.3	4.6	3.7	7.4	6.4	4.6
Allelic richness	3.80	3.82	3.66	5.26	5.16	4.02
Number of mtDNA haplotypes						
R1	20	9		2		
R2	9	5				
R3			6			
R4			5			
R5			3			
R6		2				
R7	1	3				
R10	1	1				
R14	2					
R8, R9, and R11	1 each					
R12, R13, and R15		1 each				

^a Individual herds identified in Table A1.

^b Data for caribou from Cronin and others (2005).

CRH, BM848, CSSM036, and BMS468 loci in Scandinavia. In all these cases there were fewer heterozygotes than expected, which may reflect that our samples came from several herds in each region (i.e., a Wahlund effect). No pairs of loci had significant ($P > 0.0003$) nonrandom associations of genotypes, indicating the loci are not linked. The distribution of microsatellite alleles shows there is significant differentiation among the 3 regions indicated by an F_{st} higher than zero ($F_{st} = 0.073$, 95% confidence interval [CI] 0.052–0.095). Pairwise F_{st} values indicate relatively low level of differentiation between Alaska and Russia ($F_{st} = 0.053$, 95% CI 0.025–0.084) and more differentiation between Alaska and Scandinavia ($F_{st} = 0.100$, 95% CI 0.059–0.144) and Russia and Scandinavia ($F_{st} = 0.121$, 95% CI 0.084–0.158).

Comparison of Reindeer and Wild Caribou

Different mtDNA haplotypes occur in reindeer and caribou with one exception: 2 caribou in Alaska had haplotype R1, probably because of introgressive hybridization from rein-

deer to wild caribou. This is 2.6% of the 78 Alaskan caribou for which mtDNA haplotypes were determined. Forty-five mtDNA haplotypes observed in Alaskan barren-ground caribou, 10 haplotypes in Canadian barren-ground caribou, and 8 haplotypes in woodland caribou (Cronin and others 2005) were not observed in any of the reindeer herds.

There are more microsatellite alleles and higher allelic richness in barren-ground caribou than reindeer (Table 1). Allelic richness was significantly higher ($P < 0.05$) in the Alaskan and Canadian barren-ground caribou than in the Alaskan reindeer, Russian reindeer, Scandinavian reindeer, and woodland caribou. Genetic distances (Table 2) of microsatellite allele frequencies indicate similarity of Alaskan and Russian reindeer, and of Alaskan and Canadian barren-ground caribou, and differentiation of these groups and woodland caribou and Scandinavian reindeer. These relationships are shown in the dendrogram (Figure 2B) in which the Alaskan and Russian reindeer occur in a cluster, the Alaskan and Canadian barren-ground caribou occur in a cluster, and the woodland caribou and Scandinavian reindeer cluster outside these groups.

Table 2. Genetic distances (Cavalli-Sforza and Edwards 1967) between reindeer and caribou

	Alaskan reindeer	Russian reindeer	Scandinavian reindeer	Alaskan caribou	Canadian caribou	Woodland caribou
Alaskan reindeer						
Russian reindeer	0.200					
Scandinavian reindeer	0.347	0.358				
Alaskan barren-ground caribou	0.263	0.297	0.311			
Canadian barren-ground caribou	0.306	0.310	0.333	0.220		
Woodland caribou	0.307	0.319	0.327	0.276	0.321	

Discussion

Reindeer in Alaska have levels of genetic variation and mtDNA haplotype and microsatellite allele frequencies comparable to herds in the geographic region of origin, Siberia, Russia, more than 100 years after their introduction. This is despite repeated founder events as animals were introduced from Siberia to the Seward Peninsula and then dispersed to establish other herds. We do not know the relationship of our Russian samples and the source herds of the Alaskan samples, but our results suggest they share recent common ancestry. The large number of founders (1280 animals) and rapid herd growth following introduction may have maintained genetic variation in Alaskan reindeer. In contrast, the Svalbard Island reindeer have low genetic variation (Table A1, Røed and Whitten 1986; Gravlund and others 1998; Côté and others 2002).

Microsatellite allele and mtDNA haplotype frequencies are differentiated between the Alaskan/Russian reindeer and wild caribou in Alaska (Table 2, Figure 2B). Our results and those of others (Røed and Whitten 1986; Cronin and others 1995) suggest that introgressive hybridization between reindeer and wild caribou has been limited despite extensive mixing of reindeer and caribou herds in western Alaska (Bailey and Hendee 1926; Rausch 1951; Klein 1980; Stern and others 1980). A low frequency of reindeer mtDNA haplotypes in caribou (2.6%) indicates some female-mediated gene flow. The similarity of the Alaskan and Canadian barren-ground caribou (Figure 2B) also suggests that the Alaskan

caribou have maintained native genetic structure with limited reindeer influence.

Our results show patterns of differentiation that reflect population histories. The polyphyletic mtDNA relationships of the Alaskan/Russian reindeer and barren-ground caribou suggest recent common ancestry during the last (Wisconsin) glaciation when the Bering land bridge connected Siberia and Alaska. However, postglacial restriction of gene flow is indicated by different mtDNA haplotypes and microsatellite allele frequencies in reindeer and caribou. The Russian reindeer (and Alaskan transplants) may represent populations isolated postglacially on the Asian side of the Bering Strait (with subsequent domestication), while the Alaskan and Canadian caribou represent populations on the North American side. The unique mtDNA haplotypes and differentiated microsatellite allele frequencies of woodland caribou and Scandinavian reindeer probably resulted from isolation south of the North American continental glaciers and in a northern European glacial refugium, respectively (Røed and Whitten 1986; Røed and others 1991; Cronin 1992; Gravlund and others 1998; Courtois and others 2003; Flagstad and Røed 2003).

The domestication of reindeer in Eurasia may have been accompanied by founder effects, genetic drift, and selection that may have resulted in lower levels of genetic variation in reindeer than large, wild caribou populations with high levels of gene flow. However, the reindeer herds in Alaska and Siberia appear to have considerable levels of genetic variation, probably maintained with adequate numbers of animals in herd introductions and management.

Appendix

Table A1. Measures of genetic variation for 18 microsatellite loci and mtDNA in reindeer herds

Herd	Microsatellites					mtDNA	
	<i>N</i>	<i>H_e</i>	<i>H_o</i>	<i>A</i>	Allelic richness	<i>N</i>	Number of genotypes
Alaskan reindeer ^a							
Hagemeister Island	19	0.448	0.456	3.7	1.45	6	3
Tom Gray	23	0.413	0.387	3.8	1.41	11	5
Nunivak Island	15	0.387	0.344	3.2	1.39	6	2
St Lawrence Island	10	0.352	0.325	2.5	1.35	5	2
Davis	4	0.419	0.389	2.4	1.42	4	3
Noyakuk	2	0.472	0.389	1.8	1.47	2	2
Pribilof Islands	2	0.454	0.361	1.9	1.45	2	2
Russian reindeer							
Severoevensk	43	0.415	0.375	4.4	1.42	21	8
Pevek	3	0.426	0.402	2	1.46	1	1
Wrangel Island	5	0.477	0.382	2.9	1.51	1	1
Scandinavian reindeer							
Sweden	1	0.444	0.444	1.4	1.44	1	1
Norway	11	0.432	0.364	3.0	1.43	11	2
Svalbard Island	7	0.255	0.302	1.9	1.26	5	1

^a The Davis, Noyakuk, and Tom Gray herds are on the Seward Peninsula, Alaska. The Nunivak Island herd started with a transplant of 81 reindeer from the Seward Peninsula in the early 1900s (Stern and others 1980). The Hagemeister Island herd originated with a transplant of 71 animals from the Nunivak Island herd in 1965. An additional 73 females from Nunivak Island were introduced to Hagemeister Island in 1967 (Lay 1994). The establishment of the Alaskan herds on St Lawrence Island and the Pribilof Islands and movements among them are not well documented. Reindeer steers were also brought to Alaska from Scandinavia in 1897 but would not have contributed to the gene pool (Stern and others 1980).

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